

The effects of introduced tilapias on native biodiversity

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ABSTRACT

1. The common name ‘tilapia’ refers to a group of tropical freshwater fish in the family Cichlidae (*Oreochromis*, *Tilapia*, and *Sarotherodon* spp.) that are indigenous to Africa and the southwestern Middle East. Since the 1930s, tilapias have been intentionally dispersed worldwide for the biological control of aquatic weeds and insects, as baitfish for certain capture fisheries, for aquaria, and as a food fish. They have most recently been promoted as an important source of protein that could provide food security for developing countries without the environmental problems associated with terrestrial agriculture. In addition, market demand for tilapia in developed countries such as the United States is growing rapidly.

2. Tilapias are well-suited to aquaculture because they are highly prolific and tolerant to a range of environmental conditions. They have come to be known as the ‘aquatic chicken’ because of their potential as an affordable, high-yield source of protein that can be easily raised in a range of environments — from subsistence or ‘backyard’ units to intensive fish hatcheries. In some countries, particularly in Asia, nearly all of the introduced tilapias produced are consumed domestically; tilapias have contributed to basic food security for such societies.

3. This review indicates that tilapia species are highly invasive and exist under feral conditions in every nation in which they have been cultured or introduced. Thus, the authors have concluded that, despite potential or observed benefits to human society, tilapia aquaculture and open-water introductions cannot continue unchecked without further exacerbating damage to native fish species and biodiversity. Recommendations include restricting tilapia culture to carefully managed, contained ponds, although exclusion is preferred when it is feasible. Research into culture of indigenous species is also recommended.

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KEY WORDS: aquaculture; invasive; *Oreochromis*; tilapia; fish; fisheries; biodiversity; exotics; freshwater

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INTRODUCTION

Tilapiine fishes, often collectively called tilapias, are a group of subtropical to tropical freshwater fish of the family Cichlidae that are native to Africa and the south-western Middle East. Tilapias are grouped into three genera according to parental care patterns: *Oreochromis* (arena-spawning maternal mouthbrooders), *Sarotherodon* (paternal or biparental mouthbrooders), and *Tilapia* (substrate spawners). Since the 1930s, many tilapia species have been intentionally dispersed almost worldwide. Tilapias have been introduced primarily for the following reasons: for the biological control of aquatic weeds and insects, as baitfish for certain capture fisheries, as a food fish in aquaculture systems, as aquarium species, and to augment capture fisheries.

Tilapias may be introduced to natural aquatic ecosystems where they are not native by any of the above-mentioned types of activities. Of particular concern is the promotion of aquaculture, which has led to unintended consequences in several cases. Aquaculture is generally defined as the farming of fish, shellfish, or aquatic plants; however, production practices vary widely. Freshwater finfish, such as tilapia, are often grown in closed systems, such as inland ponds. However, development agencies and other organizations are increasingly using floating cages to grow tilapias in open water bodies throughout the tropics; escapes are inevitable from this technology (McCrary *et al.*, 2001). In rural Southeast Asian communities, integrated rice and fish culture is promoted, and farmers stock their rice paddies with carps and tilapias. Fish often wash out of fields flooded by rains and may escape into natural waters (IIRR *et al.*, 2001). This paper considers all types of tilapia introductions into areas where they are not native, including intentional and unintentional introductions via cage and pond culture, fishery stock enhancement (stocking), and use for biological control, bait, and hobby aquaria.

Certain tilapias, such as Nile and Mozambique tilapias (*Oreochromis niloticus* and *Oreochromis mossambicus*, respectively) are well-suited to aquaculture production because they are fast-growing and tolerant of a range of environmental conditions. These species adapt readily to changes in salinity levels and oxygen availability, can feed at different trophic levels, and, under certain circumstances, can tolerate overcrowding (McKaye *et al.*, 1995; Courtenay, 1997; Coward and Little, 2001). Tilapias are also known to occupy both freshwater and estuarine environments within their native ranges (Trewavas, 1983), and some species have become invasive in both types of systems in other countries. While these attributes benefit the aquaculturist, their wide environmental tolerances, trophic adaptability, and high reproductive rates predispose tilapias for success as invasive species (Trewavas, 1983; Ehrlich, 1988). In fact, the current distribution of tilapias as a group is virtually pan-tropical. They are probably the most widely distributed group of exotic fish worldwide, and have become established in nearly every water body in which they are cultured or have otherwise gained access (Courtenay, 1997; Costa-Pierce, 2003).

This paper examines the impacts of tilapia introduced through aquaculture or other means on native fish and their habitats. It is not intended as a comprehensive review, but rather as a description of the potential effects of introduced tilapia species on native biodiversity. The target audience is aquaculturists, natural resource managers, and other groups pursuing or considering the culture or introduction of tilapias. The paper presents background information on the history and current status of tilapia aquaculture, highlights several of the key environmental issues with tilapia aquaculture, provides an analysis of selected case studies, and identifies priorities for future research and policy development.

HISTORY OF TILAPIA INTRODUCTIONS AND AQUACULTURE

Shafland and Lewis (1984) defined introduced species as: 'any species intentionally or accidentally transported and released by humans into an environment where it was previously absent'. This definition includes species moved to areas outside their geographic range, as well as transfer or translocation of

species within their geographic ranges to systems they previously did not inhabit. However, introduced species are not always considered invasive. An invasive alien species (or an invasive species) is defined by the Convention on Biological Diversity as: ‘an alien species (a species, subspecies, or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce), whose introduction and/or spread threaten biological diversity’ (Ciruna *et al.*, 2004).

The first introduction and establishment of non-native tilapias is believed to have occurred in Java (Indonesia) in the 1930s as a result of an aquarium release of Mozambique tilapia, *Oreochromis mossambicus* (Courtenay and Williams, 1992). The introduction and spread of this species continued throughout World War II, because it was an easily transported food source for Japanese soldiers (Walter Courtenay, pers. comm.). Subsequent decades saw widespread introductions of this species and other tilapias for biological control (of insects or aquatic weeds, for example), as baitfish, and from home aquaria.

During the 1960s and 1970s, international aid and development agencies promoted aquaculture as a protein production method that could improve food security for developing countries without the environmental problems associated with terrestrial agriculture. The ‘grain-to-feed conversion rates’ for fish (i.e. the amount of grain needed to produce a given quantity of meat) are equivalent to those of chicken, and far more economical than pork or beef. In the early 1980s, these agencies and others called for a ‘Blue Revolution’ (suggestive of the earlier ‘Green Revolution’ that promised to alleviate hunger through agriculture), and funded research into aquaculture practices, including selection for disease-resistant, growth-enhanced fish through conventional breeding methods (McGinn, 1998).

Today, aquaculture is often considered a sustainable replacement for wild-caught fish stocks and as a means to meet the demand for many fish commodities. According to the United Nations’ Food and Agriculture Organization (FAO) State of the World’s Fisheries and Aquaculture 2002 report, more than one billion people worldwide rely on animal protein from fish, and approximately 56% of the world’s population derives at least 20% of its animal protein intake from fish. From 1970 to 2001, the contribution of aquaculture, freshwater and marine, to the global supply of fish, crustaceans, and molluscs increased from 3.9% to 29% of total production by weight. It is projected that by 2015–2030, farm yield will exceed wild catch as world capture fishery production stagnates (FAO, 2002; Fitzsimmons, 2003).

Tilapias, in particular, have come to be known as the ‘aquatic chicken’ because of their potential as an affordable, high-yield source of protein that can be raised easily in a range of environments — from subsistence or ‘backyard’ units to intensive fish hatcheries (Coward and Little, 2001). Tilapia operations in some areas are very profitable, especially where consumer acceptance is high and production practices are managed efficiently. In 1993, researchers in the Philippines announced a strain of Nile tilapia that grew 60% faster than its wild relatives. Through the Genetic Improvement of Farmed Tilapia (GIFT) programme, the World Fish Center demonstrated that selection for faster-growing fish could yield significant increases in growth of tilapia and substantial improvements in production. Significant research and funding have been invested in improving the performance and farming efficiency of GIFT tilapia, and they have been used and studied widely in Asia (Dey *et al.*, 2000).

Although the net worth of the aquaculture industry is dominated by high-value carnivorous species, production in volume is dominated primarily by freshwater, herbivorous fish, including carps, catfishes, milkfishes, tilapias, and shellfish (McGinn, 1998). Tilapia aquaculture has undergone a period of rapid growth, particularly in Africa, Asia, and some parts of Latin America. The most important tilapias in aquaculture are species in the mouthbrooding genus *Oreochromis* — *O. niloticus*, *O. mossambicus*, and *O. aureus* — and certain hybrids, which account for 99.5% of global tilapia production (FAO, 1997). However, species from all three genera — *Oreochromis*, *Sarotherodon*, and *Tilapia* — are utilized in aquaculture and for fishery stock enhancement by direct introductions.

Since the 1980s, nearly all worldwide introductions of tilapias have been for aquaculture. Tilapias are the third most widely farmed fish in the world (after carps and certain salmonids), with a global production of

1.49 million metric tons in 2002 (Fitzsimmons, 2003). In 2002, approximately 70% of world farmed tilapia production came from Asia; and 46% from China alone (Fitzsimmons, 2003). While aquaculture production in Africa has been slower in its growth, it has risen from 37 000 metric tons in 1984 to 189 000 in 1998, with the majority of this production from carps and tilapia (FAO, 2000). It should be noted that there are some examples of tilapia introductions for cultivation that have failed initially (McCrary *et al.*, 2001); in such cases, however, subsequent introductions have typically resulted in establishment (Ken McKaye, pers. comm.). Throughout the Caribbean, tilapias have been introduced for aquaculture but, with the exception of Jamaica and Cuba, most projects have been terminated (Hargreaves and Alston, 1991).

Nile and Mozambique tilapias are the most widely distributed. Nile tilapia dominates global tilapia aquaculture, accounting for 72%, or 474 metric tons, in 1995 (FAO, 1997). Other tilapias used in aquaculture include: blue tilapia (*Oreochromis aureus*), mango tilapia (*Sarotherodon galilaeus*), longfin tilapia (*Oreochromis macrochir*), redbreast tilapia (*Tilapia rendalli*), and the hybrid Mozambique–Wami River tilapia (*O. mossambicus* × *O. urolepis hornorum*). The red hybrid tilapia (*O. mossambicus* × *O. niloticus*) is also being produced for aquaculture (Aiken *et al.*, 2002; Hashim *et al.*, 2002). The blue, the Mozambique, the Nile, and the Mozambique × Wami hybrid are widely employed in aquaculture in the Americas, and all have been reported as established in the wild. Populations of spotted tilapia (*Tilapia mariae*), blackchin tilapia (*Sarotherodon melanotheron*), longfin tilapia, redbreast tilapia, and redbelly tilapia (*Tilapia zillii*) have also been established in US waters (Courtenay, 1997) and *T. mariae* has become established in northern Australia (Arthington, 1991).

AQUATIC INTRODUCTIONS: REASONS FOR CONCERN

According to the FAO Database on Introductions of Aquatic Species (www.fao.org/waicent/faoinfo/fishery/statist/fisoft/dias/mainpage.htm), most introductions of aquatic species occurred as a consequence of aquaculture or as part of a stocking or fishery enhancement effort. In general, introduction of a species into a country for aquaculture purposes does not necessarily imply its introduction into natural waters, particularly if aquaculture is performed in closed systems. However, because the establishment of rigorous containment systems can be costly and difficult (Ricciardi and Rasmussen, 1998; Ham and Pearsons, 2001), aquaculture is frequently performed in open systems, and this implication is often correct.

Aquaculture has the potential to affect areas far beyond the site where the fish are initially cultivated. Aquaculture species frequently establish reproducing populations when they escape from the aquaculture system into suitable habitats or are introduced into the wild (Arthington and Blühdorn, 1996; Courtenay, 1997), and many have a history of rapid spread. Thus, aquaculture can be a pathway by which non-native fish or other cultivated species can become established in the native ecosystems of their host countries. This is an obvious potential outcome when non-native species are introduced directly into open waters for stock enhancement or for other reasons, such as biological control. However, there is also the potential for fish to escape from culture cages, and even from carefully managed ‘closed’ systems, through effluent drainage systems or as the result of a weather event, such as a flood or hurricane.

The criteria for evaluating the ‘success’ of a species introduction in natural waters, constituted by survival and possibly successful reproduction, differ among societies (Welcomme, 1984). For example, developed nations might evaluate success based on the extent to which environmental or ecosystem disturbance is minimized while the goals of the introduction are achieved, whereas developing countries might tolerate such disturbances in favour of increased food production (Ferguson, 1990). It is important to understand the relationship between economic choices and potential impacts on ecosystem health, so that economic incentives can be used to prevent or limit the impacts of invasive species and ensure that both ecosystems and economies are safeguarded.

The introduction of invasive species is widely considered to be a leading cause of species endangerment and extinction in freshwater systems (Claudi and Leach, 1999; Harrison and Stiasny, 1999; Sala *et al.*, 2000). In fact, invasive species are regarded as the second leading cause of species extinction and endangerment worldwide, following habitat destruction. Invasive species are thought to cause or contribute to more than 70% of native North American freshwater species extinctions during the twentieth century (Williams *et al.*, 1989). A survey of 31 fish introduction studies in Europe, North America, Australia, and New Zealand found that, in 77% of the cases, native fish populations were reduced or eliminated following the introduction of alien fish species (Ross, 1991). Of Mexico's roughly 500 freshwater fish, 167 species have been listed as being at some degree of risk, and 76 of these are the result, at least in part, of invasive species (Contreras-Balderas *et al.*, 2002). In Australia, invasive, non-native fish species are one of the leading causes in the decline of 22 species of native fish that are classified as endangered, vulnerable, or rare (Wager and Jackson, 1993).

The ecological impacts of invasive species on inland water ecosystems vary significantly depending on the invading species, the extent of the invasion, and the vulnerability of the ecosystem being invaded. Loss and degradation of biodiversity caused by invasive species can occur throughout all levels of biological organization from the genetic and population levels to the species, community, and habitat/ecosystem levels. Impacts can vary in terms of their severity, interaction with other threats, and ability to cascade throughout an entire ecosystem (Wilcove *et al.*, 1998; Levine, 2000; McNeely, 2001).

Invasive species generally reduce native inland water species abundance through predation, hybridization, parasitism, or competition and may alter community structure and ecosystem processes, such as nutrient cycling and energy flow or, in the case of invasive plants, the hydrologic regime of a particular inland water aquatic ecosystem (Arthington, 1991; Bunn *et al.*, 1997, 1998). Their effects on inland water ecosystems can be grouped into eight general categories: alteration of hydrologic regime; alteration of water chemistry regime; alteration of physical habitat; alteration of habitat connectivity; impacts on the biological community; impacts on specific populations; genetic impacts; and alteration of ecosystem structure and processes (e.g. food web structure and energy flow). The summary and case studies that follow examine some of these impacts with regard to tilapias.

TILAPIA INTRODUCTIONS: A SUMMARY OF POTENTIAL IMPACTS

Tilapias are feral in every nation in which they have been cultured or introduced and where local conditions allow their establishment (Courtenay, 1997; Costa-Pierce, 2003). This includes establishment in natural environments as well as artificial ones, such as reservoirs or areas where power plants create thermal refugia in natural waters. Despite this, a systematic approach to assessing the potential environmental impacts of tilapia introductions has yet to emerge. Decisions and statements about new tilapia introductions are frequently based on guesswork and extrapolation, and advocates and opponents are polarized, with both sometimes overstating their case (Pullin *et al.*, 1997).

This is cause for concern, considering that tilapias clearly demonstrate characteristics shared by many successful invasive species. Most widely reported is their ability to exclude native fish from prime breeding grounds. In addition, tilapias are reproductively active for long periods, in some places for most of the year. They have short reproductive cycles and have been observed to spawn year-round in the wild with a higher frequency than most fish (Walter Courtenay, Ken McKaye, Mark Peterson, and Jay Stauffer, pers. comm.). They are also highly protective of their young: nest-building *Tilapia* species guard fertilized eggs in the nest, while mouth-brooding species of *Sarotherodon* and *Oreochromis* fertilize eggs in brooding platforms, called bowers (McKaye *et al.*, 2001), then carry them by mouth through incubation and for several days or more after hatching (Jay Stauffer, pers. comm.). Mouthbrooders do not have strict habitat requirements for reproduction, so they can occupy all available habitat within their spawning sites (McKaye *et al.*, 1995).

For example, a maternal mouthbrooder (such as a species of *Oreochromis* spp.) can colonize a new environment by carrying her young in her mouth (Fryer and Iles, 1972).

Trophic interactions are also important. Whereas tilapias are generally considered herbivores, detritivores, or planktivores, they have been documented to consume the eggs and larvae of other fish species, and even small fish (Arthington *et al.*, 1994; USFWS, 2002). Certain tilapias are known to be omnivorous, with their feeding habits changing depending on season and locality (Arthington *et al.*, 1994). Juvenile tilapias, in particular, are known to feed on smaller fish (de Moor *et al.*, 1986). Further, Crutchfield (1995) reported direct, negative trophic interactions on native species associated with accidental introduction of redbelly tilapia in a power plant reservoir in North Carolina. The redbelly tilapia became the fourth most abundant species in the reservoir within 3 years of introduction — its feeding habits eliminated all submerged and floating aquatic macrophytes within 2 years, which coincided with significant declines in populations of four common and abundant species of native fish. Similar impacts have also been documented in Lake Apoyo, Nicaragua, where Nile tilapia have fed on and eliminated *Chara* spp., an important plant habitat for native cichlids (McCrary *et al.*, 2001).

In lakes Victoria and Kyoga (Africa), introduction of *O. niloticus* is linked to the decline of native *Oreochromis esculentus* and *Oreochromis variabilis* (Twongo, 1995; Goudswaard *et al.*, 2002). This is attributed to several dynamics, including a change in trophic interactions resulting from the introduction of more than one non-native species. According to Ogutu-Ohwayo (1990), *Lates niloticus*, *O. niloticus*, and two other cichlids were introduced into Lake Victoria in the 1950s and early 1960s; *L. niloticus* and *O. niloticus* at present dominate the fish fauna, although recent studies show that these populations are declining and that a portion of the indigenous fish fauna is now resurging (Balirwa *et al.*, 2003; Chapman *et al.*, 2003). *L. niloticus* is a piscivore and is believed to have eliminated many native haplochromine cichlids in the lake; *O. niloticus* is primarily herbivorous. Because the decline of haplochromine cichlids has altered lake productivity, *O. niloticus* now outcompetes certain remaining cichlids, two of which are tilapiine (Ogutu-Ohwayo, 1990).

Another potential impact of tilapia introductions is eutrophication, a process through which enrichment with nutrients such as nitrogen and phosphorus leads to increased production of organic matter (Armantrout, 1998). Eutrophication can result in suffocating algal blooms, growth of toxic algae, and fish die-offs (fish kills). Because intensively fed fish generate faecal and other wastes, e.g. from uneaten food, any intensive aquaculture operation, including intensive tilapia farming, can cause nutrient enrichment of water and eutrophication. While this cause and effect is not unique to tilapia culture, Starling *et al.* (2002) have demonstrated a linkage between the high tilapia biomass in Lago Paranoá, a tropical reservoir in Brazil, and increases in total phosphorus (a result of P-release from bioturbation and excretion), chlorophyll *a*, and cyanobacteria (blue-green) concentrations. They attribute this to 'ichthyoeutrophication' by tilapia foraging on benthic algae, reporting that bioturbation and nutrient recycling through ingestion and excretion have dramatically increased the bioavailability of nutrients in this system.

There is also concern about the genetic impacts of introduced tilapia on native cichlid populations. Carvalho and Hauser (1995) divide genetic impacts into two categories: direct impacts that initiate changes in gene flow (hybridization and introgression), and indirect impacts, such as a decline in population size of the indigenous species resulting in the loss of locally adapted populations and of genetic diversity. Tilapia stocks have been moved repeatedly and allowed to interbreed with local populations, which in some cases has resulted in decreased genetic diversity and 'pollution' of endemic populations (Fitzsimmons, 2001).

TILAPIA INTRODUCTIONS: CASE STUDIES

A review of the literature related to the effects of non-native tilapia introductions on biodiversity suggests that such introductions have effects on native fish populations. In general, aquatic ecosystems have been

poorly studied prior to tilapia introductions. However, in certain well-studied cases impacts on native fish populations have been clearly demonstrated — for example, in Lake Victoria, where Nile tilapias are thought to have outcompeted or genetically subsumed two native cichlids (Twongo, 1995; Goudswaard *et al.*, 2002), and in Nicaragua (McKaye *et al.*, 1995; McKaye *et al.*, 1998b). In most cases, the lack of baseline data and the influence of human impacts and alterations within ecosystems make it difficult to conclude that tilapia were the primary causal agents in the decline of native species or their habitats. As mentioned previously, the issue is further confounded by differences of opinion as to whether tilapias are a pest or an important food fish, and biases inherent in this debate affect research and reporting.

A body of literature documenting the establishment of tilapia populations — and in some cases impacts of tilapia on native biodiversity — is emerging from around the world (see Appendix). The literature demonstrates that, owing to their adaptability to various water conditions, prolific breeding habits and territoriality, as well as their ability to feed at a range of trophic levels, tilapias typically outcompete native species for food, habitat, and spawning sites, and thus displace native species in rivers, lakes, and estuaries. In addition, tilapias, especially *O. mossambicus* and its hybrids, are euryhaline and can therefore invade estuarine and nearshore marine ecosystems (Costa-Pierce and Riedel, 2000). In some cases, the only evidence of an impact is reports from local fishermen of a correlation between the introduction of tilapias and a decline in native fish. The case studies that follow illustrate some of the potential and actual effects of tilapia introductions on native fish and show where future research may be needed.

Africa: Kafue and Zambezi basins

The Zambian Government's Department of Fisheries first approved the introduction of Nile tilapias (*O. niloticus*) for aquaculture around the 1960s; they were subsequently brought into Zambia for cage culture in Lake Kariba and to fish farms in the Kafue River catchment, both in the Middle Zambezi system. Today, *O. niloticus* is widely distributed in Zambia and is reared by commercial and small-scale farmers on Lake Kariba and in parts of the Kafue and Congo basins. Over 10 000 fish farmers in Zambia possess various tilapia species, including Nile tilapias. Large-scale commercial farmers use a variety of aquaculture systems, including cages, tanks, large semi-intensive ponds, and raceways; almost all grow Nile tilapias. Government fish stations in Northern Province, Copperbelt, Northwestern, Central, and Lusaka Provinces maintain, multiply, and distribute Nile tilapias to farmers (Maguswi, 1992; Woynarovich, 1995; Mwango *et al.*, 1999; Soma *et al.*, 1999).

According to the South African Institute for Aquatic Biodiversity (Denis Tweddle, pers. comm.), *O. niloticus* has escaped from culture ponds into the Lake Kariba and Kafue systems and successfully reproduced. Further introductions have taken place in reservoirs in Zimbabwe, so that *O. niloticus* is now also established in the Limpopo River system, where they are hybridizing with indigenous Mozambique tilapia (*O. mossambicus*). The primary concern in the Limpopo River system is the replacement of native *O. mossambicus* with red hybrid populations (*O. niloticus* × *O. mossambicus*) throughout the natural range of the Mozambique tilapia, and the subsequent loss of genetic integrity (van der Waal and Bills, 2000). Researchers conducting Upper Zambezi surveys are thus concerned about an active US cooperative technical assistance programme to develop aquaculture of *O. niloticus* in the Upper Zambezi system in northern Zambia (Denis Tweddle, pers. comm.). At a fish farm that is part of the project, they found ponds stocked with a mixture of *O. niloticus* and a hybrid between the *O. niloticus* and the indigenous three-spot tilapia (*Oreochromis andersonii*). Approximately 250 ponds have been stocked with *O. niloticus* in the Upper Zambezi catchment.

Many workers have shown that growth of the native three-spot tilapia (*O. andersonii*) is superior in pond culture to that of other native tilapias (e.g. *T. rendalli* and *O. macrochir*) (Maguswi, 1992; Banda, 1993; Jensen and Mugala, 1993; Mulenga, 1993; Wijkstrom and Wahlstrom, 1993; Crayon-Thomas, 1994; Evans, 1994; Maguswi, 1994; Vuren and Steyn, 1994; Woynarovich, 1995). While experts disagree about

whether *O. andersonii* is superior to *O. niloticus* as candidate fish for aquaculture programmes in this region, there is probably no strong justification for promoting the use of non-native *O. niloticus* in the region. The situation is complicated by the fact that *O. andersonii* is native only to the Kafue and Zambezi basins and not in other areas of Zambia, where other tilapia species should be considered.

Lack of available data on the native tilapias, in addition to limited technical capacity, facilities, and financial resources, have made it difficult for the Zambian Department of Fisheries to conduct trials of the aquaculture potential of native fish species. Fast growth and high performance of *O. niloticus* have been the main justification for its candidature, introduction, and continued use in Zambia (as is the case in other countries as well) (Evans, 1994; Moehl *et al.*, 1995; Mohl, 1995; Irvine and Mulonda, 1996; FAO, 2000).

Farmers in Botswana, the Democratic Republic of the Congo, Mozambique, Namibia, Zambia, and Zimbabwe, are all reportedly producing *O. niloticus* in farming areas that drain into shared waters. Regional mechanisms have not yet been established to provide for cooperation in areas beyond national jurisdictions (Bartley, 1993; Bartley and Coates, 1994; de Moor, 1994; Maes, 1994; Sen, 1994; van der Audenaerde, 1994). Active promotion of *O. niloticus* culture in this region increases the risk of introduction of these non-native species into shared waters. There is a clear need for greater cooperation among these countries on issues pertaining to the introduction of aquatic species into, or near, river systems that cross national boundaries.

Australia

Mozambique tilapia, *O. mossambicus*, were first recorded in the wild in the early 1980s in two water supply reservoirs (North Pine Dam and Leslie Harrison Dam) in the Brisbane region of south-east Queensland, as well as the streams below these dams (McNee, 1990; Arthington and Blühdorn, 1994). The species has also been reported in Lake Wivenhoe, the impoundment behind Wivenhoe Dam situated on the middle Brisbane River, and in the Brisbane River itself (McNee, 1990). These populations are cause for concern due to the risk of inter-basin transfers via a water supply pipeline constructed to deliver water from Wivenhoe Dam to more northern river basins experiencing water shortages. The translocation of tilapias into northern catchments would threaten river systems with rich indigenous faunas and relatively few non-native fish and, to date, without any known records of *O. mossambicus*. At stake, according to some authorities, is the Australian lungfish, *Neoceratodus forsteri*, recently declared 'vulnerable' under section 78 of the Environmental Protection and Biodiversity Conservation Act (Pusey *et al.*, 2004). Preventive measures, such as control of water off-take position, screens, and regular inspections may not be sufficient to detect and prevent inter-basin transfers of very small *O. mossambicus* via the Wivenhoe pipeline, even though considerable effort is being invested in such strategies and related research.

In Townsville, Queensland, *O. mossambicus* is present in urban drains, several small creeks, and the Ross River (McNee, 1990), whereas in Cairns this tilapia inhabits coastal waterways and small estuaries (Arthington and Blühdorn, 1994). *O. mossambicus* has been recorded in several streams flowing into Lake Tinaroo on the Atherton Tableland near Cairns and one population is present in the lake itself (Alf Hogan, pers. comm.). Tinaroo Falls Dam overflowed in the early 1999 floods; hence the species' distribution could be more extensive (Brad Pusey, pers. comm.). *O. mossambicus* is present in the lower Barron River; a very large population occurs in Freshwater Creek below the Barron River Falls and is now distributed a considerable distance further up the escarpment, where its distribution appears to be limited by gradient only (McNee, 1990; Brad Pusey, pers. comm.). South of Cairns, *O. mossambicus* has become established in the lower Mulgrave River and the lower North and South Johnstone rivers (Russell and Hales, 1993). These populations extend more widely than their earlier focus around the effluent outlets of sugar mills (Brad Pusey, pers. comm.). An attempted eradication of this species from a small reservoir in Rockhampton has evidently failed.

A population of *O. mossambicus* is well-established in the Gascoyne–Lyons River system, Western Australia (McNee, 1990; Arthington and Blühdorn, 1994). This population originated from fish released into the Gascoyne River at Carnarvon, and in less than 10 years *O. mossambicus* had invaded almost the entire accessible length of this arid zone river system (Arthington and Blühdorn, 1994).

Feral tilapias in Australia are believed to have resulted from 1970s introductions of a small number of progenitors from aquarium stocks, probably originating in Singapore or Indonesia. Feral populations were assumed to belong to one common tilapia species, *O. mossambicus*, although other closely related cichlids were brought to Australia during the same period by aquarists (McKay, 1978). An electrophoretic analysis of *O. mossambicus* populations in Australia has identified two distinct genetic strains, a common southern strain found in Brisbane, Townsville, and the Gascoyne–Lyons system, and a northern strain found only in the vicinity of Cairns (Mather and Arthington, 1991). The southern strain is a relatively pure form of *O. mossambicus*, although the fish from the Gascoyne–Lyons system have a lower level of genetic variability than populations established in eastern Australia. The northern strain from Cairns is polymorphic at three enzyme loci that are monomorphic in the southern populations. The discovery of distinct genetic strains in Australian populations of *O. mossambicus* is significant because this species has relatively low levels of genetic variability compared with other tilapia species (McAndrew and Majumdar, 1983).

Mather and Arthington (1991) consider that the polymorphic strain is an interspecies hybrid based on *O. mossambicus* but with genes from at least one or more of *O. niloticus*, *O. hornorum*, and *O. aureus*. Hybridization is likely to have taken place in captivity prior to the importation of *O. mossambicus* into Australia. Already the hybrid northern strain is spreading in wetlands, streams and larger rivers around Townsville and Cairns, including protected streams in the Wet Tropics World Heritage Area (Arthington *et al.*, 1999). Potential impacts of *O. mossambicus* are reviewed in Arthington and Blühdorn (1994, 1996).

The record of *O. mossambicus* as an invasive species in other countries has led to the declaration of 'noxious' status in Queensland, and there are heavy penalties for catching, holding, transporting, and breeding this species. Several eradications have been attempted but all appear to have failed except in isolated outdoor ponds and pools. A renewed effort is under way to prevent the spread of populations at present residing in Lake Tinaroo across the divide into near-pristine rivers draining into the Gulf of Carpentaria.

Madagascar

Madagascar is important as a centre of endemism for many groups of organisms, including several freshwater taxa. It is estimated that 80% of plant and animal species in Madagascar are endemic (> 90% for forest species) (Benstead *et al.*, 2003). Certain freshwater and euryhaline fishes are highly endemic; some representatives (Cichlidae, Bedotiidae) occupy basal phylogenetic positions, making them important for evolutionary and other studies (Reinthal and Stiassny, 1991; Lévêque, 1997). Deforestation, overfishing and the introduction of exotic species are affecting many native fish species to the extent that freshwater fish are considered the most threatened of Madagascar's vertebrate taxa (Benstead *et al.*, 2003).

The main threats to Madagascar's endemic fish are deforestation and exotic species introductions. While many species have been introduced in Madagascar for aquaculture or to enhance production in natural waters, their potential impact on endemics has largely been ignored. Introduced tilapiine fishes include *O. mossambicus*, *O. niloticus*, *O. macrochir*, *Tilapia melanopleura*, *T. rendalli*, and *T. zillii*. These species were introduced to support a commercial fishing industry starting in the late 1950s. All of these species are now established and most are widespread in Madagascar (Reinthal and Stiassny, 1991; Benstead *et al.*, 2003).

There is a strong correlation between the introduction of exotic fish and the decline of native fish in Madagascar (Reinthal and Stiassny, 1991; Lévêque, 1997; Benstead *et al.*, 2003; Sparks and Stiassny, 2003). Interviews with Lake Itasy fishermen indicated that the decline of native species in the lake was correlated with the introduction of exotic species (Reinthal and Stiassny, 1991). According to Lévêque (1997), 'the

decline of the native *Ptychochromoides betsileanus* in Lake Itasy is attributed to the progressive introduction of different species, among which tilapiines are powerful competitors'. In Lake Alaotra, the progressive introductions of different species — carp first, followed by several species of tilapias in 1954 (*T. rendalli*), 1958 (*O. macrochir*), and 1961 (*O. niloticus* and *O. mossambicus*) — have also induced a drastic decline of native fish (Lévêque, 1997). Lévêque noted the quick proliferation of each of the tilapias since the first introduction in 1954, attributed to their high fecundity and ability to occupy empty niches.

Nicaragua

Fernando (1991) called early predictions of dire consequences of tilapia introductions into Central America 'groundless'. Yet, impacts from the introduction, establishment, and spread of tilapia in Nicaragua on the native freshwater and marine biota in the region have been demonstrated (McKaye *et al.*, 1995, 1998b; McCrary *et al.*, 2001), particularly in Lake Nicaragua and Lake Apoyo. Lake Apoyo and several other crater lakes in Nicaragua are biologically distinctive within the region owing to the endemic flocks of cichlids that live within their waters, and present a unique model for speciation scenarios (Stauffer *et al.*, 1995; McKaye *et al.*, 1998a; Wilson *et al.*, 2000; McKaye *et al.*, 2002).

Lake Nicaragua is part of a freshwater ecosystem connected with the Caribbean coast of Nicaragua, notable for its high biological productivity and diversity (McKaye *et al.*, 1995). Levels of endemism among fish in the catchment are extremely high (Bussing, 1998). The Rio San Juan connects the system to the Caribbean Sea, and both Lake Nicaragua and the Rio San Juan have long been considered strategically important as a link between the Atlantic and Pacific oceans in Central America. In 1983–84, an attempt to increase the fishery and create an export market led to extensive stocking of introduced African *Oreochromis* species in Lake Nicaragua and cage culture in a region known as the *isletas*, near Granada (a city on Lake Nicaragua). Almost simultaneously, Japanese and Russian interest in building an inter-oceanic canal through Lake Nicaragua in the 1980s stimulated research on the lake ecosystem, resulting in the collection of important baseline data prior to tilapia introductions throughout the system.

No tilapias were collected in Lake Nicaragua during the Soviet study in 1983 (McKaye *et al.*, 1995), but by 1987–88, fishermen in the Granada region began reporting tilapia catches. The fishermen correlated these catches with a decline in native cichlid catches, and this correlation was confirmed with data collected by McKaye *et al.* (1995). By 1990, three species of introduced tilapias (*O. aureus*, *O. mossambicus*, and *O. niloticus*) were being caught throughout the coastal region, including in Lake Nicaragua's outlet on the San Juan River, the southern islands of Solentiname, and the northern shore (including *isletas*). In comparison with standing crop levels in the lake before tilapia introduction, and in locations where tilapias had not yet migrated, there was approximately 80% reduction of native cichlids and a 50% reduction in total cichlid biomass (including tilapias) wherever introduced tilapias were found in Lake Nicaragua (McKaye *et al.*, 1995, 1998b).

Lake Apoyo is the largest and deepest of Nicaragua's volcanic crater lakes; it is an endorheic lake in the Pacific region of Nicaragua, near Lake Nicaragua. Aquaculture of blue tilapia (*O. aureus*) was attempted in cages in Lake Apoyo in 1983; the project was abandoned a few years later due to economic problems. Escapees were documented, but the project had few observed effects in the lake. During a second aquaculture project in 1995, hormone-treated, all-male Nile tilapia (*O. niloticus*) were introduced via cage culture. Escapees from this project, however, included fecund females. *O. niloticus* are now breeding in Lake Apoyo, and they have fed on and virtually eliminated *Chara* spp., an important plant habitat for native cichlids (McCrary *et al.*, 2001).

Philippines

Mozambique and Nile tilapias (*O. mossambicus* and *O. niloticus*) have been introduced to lakes and reservoirs in the Philippines since the mid-1950s to enhance existing fisheries. Millions of *O. niloticus* fry are

stocked annually in open waters by government agencies, and in many cases these introduced fish are now considered 'native' by local inhabitants. Escapees from this deliberate stocking, and from pond, cage, and pen aquaculture are reported to dominate some open waters (Pullin *et al.*, 1997). The fish catch data cited by Guerrero (1999) show that establishment of non-native tilapia populations in several Philippine lakes and reservoirs have been positive for fishery production and from a socio-economic perspective, but the ecological impacts of these and other tilapia introductions on native fish in the Philippines are unclear. *O. niloticus* may have contributed to the extinction of native cyprinids in Lake Lanao (Bleher, 1994) and the decline of the endemic sinarapan (*Mistichthys luzonensis*) in Lake Buhi (Maguila, 1999). However, the introduction of *O. niloticus* has not been shown to be the sole causal agent in either case, and the effects of its establishment are probably compounded by other factors. Mozambique tilapias are established in brackish water farms, rivers, swamps, and ricefields throughout the country, and there is some debate over whether they are a causal agent in the extinction of the endemic sinarapan (*M. luzonensis*) (Pullin *et al.*, 1997).

Mexico

Current estimates suggest that more than 31% of native Mexican fish species are considered at risk, in danger, or already extinct (Espinoza *et al.*, 1993). The most important factors in species loss in natural waters are habitat destruction or alterations (often by dams) and introduction of non-native species (Contreras and Escalante, 1984; Zambrano and Marcias-Garcia, 1999).

In the late 1970s and early 1980s, a nationwide food programme in Mexico advocated the use of aquaculture and resulted in creation of centres to produce fast-growing, easy-to-breed species such as tilapias for introduction to lakes and reservoirs throughout the country. Today, large, structured, well-funded breeding centres produce tons of carps and tilapias each year, and local officers determine where and when to introduce fish, with limited coordination among scientists, producers, and government (Zambrano and Marcias-Garcia, 1999). Introduced tilapias in Mexico include: *O. aureus*, *O. mossambicus*, *O. niloticus*, *O. urolepis hornorum*, *T. rendalli*, and *T. zillii* (Espinoza *et al.*, 1993). They have spread primarily through aquaculture, but also by other means. Non-native fish species are established in virtually every natural lake in Mexico and in a large number of reservoirs, particularly in Central Mexico (Zambrano and Marcias-Garcia, 1999). While there may be immediate benefits to fisheries from such introductions in Mexico, non-native tilapias have been shown to transfer parasites to native cichlids (Jimenez-Garcia *et al.*, 2001). Despite the lack of baseline data on the biology and ecology of native species in Mexico, researchers suspect that the introductions have had effects on the native flora and fauna (Zambrano and Marcias-Garcia, 1999; Jimenez-Garcia *et al.*, 2001). In Lake Chichincanab, introduced *O. mossambicus* competed strongly for habitat with an endemic cyprinodontid, threatening extinction (Fuselier, 2001), and was the dominant species (Schmitter-Soto and Caro, 1997).

Mississippi (USA)

In 2002, researchers in Mississippi completed a 2-yr study of the impacts of tilapia on native freshwater fish in southern Mississippi (Peterson *et al.*, 2002). The research focused on *O. niloticus* escapees from an aquaculture facility. The study measured spatial and temporal distribution of tilapia in Mississippi coastal catchments, influence of tilapia on the structure of the native fish community, and degree of trophic interaction among tilapia and native freshwater fish (e.g. sunfish, black bass).

Researchers in this study identified *O. niloticus* adults estimated to be 5–6 yr old, based on a comparison with age-length data from African populations (Mark Peterson, pers. comm.). Stomach analyses of *O. niloticus* by Peterson *et al.* (2002) concluded that *O. niloticus* can feed at any trophic level, including small insect stages and microcrustaceans as well as bottom sediments.

According to the researchers (Mark Peterson, pers. comm.), the observed impacts of tilapia on native fish in this study were strongly related to breeding behaviour. Aggression during mating and at spawning locations, and occupation of prime spawning locations by tilapia, resulted in lower abundance and diversity of native largemouth bass and bluegill.

Nevada and Arizona (USA)

Blue tilapias (*O. aureus*) were discovered in Muddy River, southern Nevada, in 1992 as a result of an illegal introduction. By 1996, they had dispersed throughout the river. In 1994, they were found in two basins of Lake Mead, and have since been found throughout the lake. By 2001 it was determined that they had spawned in the Virgin River (USFWS, 2002).

The decline in the number of endangered Moapa dace (*Moapa coriacea*) and Moapa White River springfish (*Crenichthys baileyi moapae*) have been correlated with the presence of tilapia. Tilapias are believed to prey on, or compete with, other native fish such as the federally endangered woundfin (*Plagopterus argentissimus*) and Virgin River chub (*Gila seminude*) (USFWS, 2002). Stomach content analyses of blue tilapias in this region obtained by the US Geological Survey indicate that they are omnivorous, feeding on a range of vegetable and animal material, including fish (USFWS, 2002).

DISCUSSION AND RECOMMENDATIONS

In the long term, the potential contribution of aquaculture to world fish supplies will probably be reduced by a number of factors, including aquaculture practices that lead to habitat destruction and biological (genetic) pollution (Naylor *et al.*, 2000) and water quality and availability. Poorly managed aquaculture has the potential to alter aquatic ecosystems irreversibly, thus destroying or diminishing the natural resource base from which aquaculture derives its productivity. According to a review of ecological interactions associated with aquaculture (Arthington and Blühdorn, 1996), escapes of cultivated organisms are inevitable, so any cultured non-native organism is potentially an invasive species. The likelihood of establishment of tilapias, especially in tropical waters, is extremely high. The impacts of species invasions are confounded by, and in some cases enhanced by, habitat destruction resulting from other human activities (e.g. construction of dams and flow regulation, urban development, and deforestation), so causal factors associated with changes in communities of native fish or vegetation may be difficult to identify. However, species interactions in some areas have clearly resulted in habitat alterations or disruptions that bring about the loss of biodiversity, genetic disturbances, and/or the introduction of diseases and parasites (Arthington and Blühdorn, 1996). While there may be compelling humanitarian arguments to exploit high-yield, low-cost sources of protein in the short term, conservation of 'environmental capital', or the natural resource base, is necessary from the viewpoint of economics and long-term sustainability (Tisdell, 1999). This argues for careful planning and monitoring of aquaculture developments.

Tilapia aquaculture and open-water species introductions cannot continue unchecked without further exacerbating damage to native fish species and biodiversity. Research in regions where tilapias have been introduced, including Africa and the Americas, suggests that tilapias are highly invasive in most areas in which they gain access. However, invasiveness is in some cases confounded by other factors including habitat destruction or previous non-native species introductions. It has been shown that tilapias threaten native species through disruptive spawning behaviour as well as trophic interactions. Their adaptability to a wide range of conditions enables certain tilapia species to occupy not only freshwater, but brackish and saltwater systems as well. Researchers with direct experience in observing the effects of established, introduced populations of tilapias on native fish will say, without exception, that no tilapia species should

be introduced into natural waters in which they are not native and in which they could become established (Walter Courtenay, Ken McKaye, Jay Stauffer, pers. comm.).

A total exclusion policy is not feasible at present in many locations. Extensive time, money, and effort have been invested in the development of improved strains, research on production and yield, and other aspects of tilapia aquaculture. It is understandably much easier and less expensive, at this point, for development agencies and others to work with a 'known quantity', using species for which there are available stocks and a body of knowledge with regard to production techniques.

A number of domestic and international organizations — such as the American Fisheries Society, the UN Food and Agriculture Organization (FAO), and the World Conservation Union, as well as other endorsers of the Nairobi Declaration (2002) — have articulated policies about, or models governing, the intentional introduction of non-native species to prevent losses caused by invasive species. These typically describe 'codes of conduct' or 'best management practices' for such introductions, and call for risk assessments prior to introductions and the creation of accessible information on invasive species. The precautionary approach has also been recommended to avoid or to minimize adverse impacts on natural resources and their environment when available information is insufficient for decision-making, or in cases of scientific uncertainty; FAO technical guidelines seek to ensure that the precautionary approach to species introduction is applied with appropriate scientific rigour (FAO, 1997). In addition, many individual countries have their own policies and regulations regarding aquatic species introductions. In general, such guidelines rely on risk assessment (a measure of the probability and potential consequences of establishment), monitoring, and containment to mitigate damage from species introductions. Although there may be some possibility of containing risks associated with aquaculture fish stocking programmes, the statistical ability to detect impacts and the resources available for risk containment are frequently insufficient, and negative impacts may not be adequately detected and contained (Ham and Pearsons, 2001).

Policy and research needs

Local and national governments as well as international organizations interested in creating sustainable fisheries for future generations have an obligation to invest in, and promote the development of, aquaculture and stocking practices using fish species that are not disruptive to the natural ecosystem. Policy developments should include a focus on the use of native species in aquaculture and stocking programmes, and an effort to minimize or eliminate the introduction of all non-native species, particularly in locations where endemic and threatened species occur. In areas where non-native tilapia species have not yet been introduced for culture or stocking programmes, stringent efforts should be made to exclude them. Towards that end, research and investment in the use of native species for aquaculture is urgently required. Knowledge of life-history traits and growth performance of potential aquaculture candidates is important for understanding the expected effects and management needs of a proposed aquaculture programme. Distribution patterns of native species should also be mapped, and this information disseminated to government workers and farmers for use in planning aquaculture programmes. There is an overwhelming need for the development of local laws and legislation that mirror aspects of the aforementioned international guidelines, and for effective local enforcement of such legislation.

For facilities that continue to raise tilapias, careful management of tilapia culture is recommended. Because tilapias are adaptable to a range of environmental conditions, they should be raised in contained ponds with no access to natural waters, preferably in regions where temperatures prohibit over-wintering in case of escape. Waste or other effluent from such facilities should be carefully managed so it does not reach natural water bodies. It would be worthwhile to investigate tilapia aquaculture facilities with no record of local establishments in order to document 'best management practices' or guidelines specific to tilapia aquaculture. Investment in such research is critical, as hybrid strains of tilapia are spreading in some

countries, e.g. Australia (Mather and Arthington, 1991), and genetically improved strains of tilapia are being developed and considered for culture and introduction in areas in which they are not yet established (World Fish Center Biodiversity and Genetic Resources Research Program 2003 Operational Plan, <http://www.worldfishcenter.org>).

Research on the effects of introduced tilapias on native biodiversity is intense in certain areas, such as Nicaragua and the southern and western United States. In other areas where tilapia culture and open-water introductions are widespread, such as parts of Latin America and Asia, significantly more research into the environmental impacts of tilapia introductions is needed. In most cases, there is little or no knowledge of baseline ecological conditions prior to the introduction of non-native species to inland aquatic ecosystems. At the ecosystem level, more data are needed to quantify the effects of invasive species on ecological processes such as food-web structure and energy flow, and the cascading impacts of non-native species, from bottom-up processes such as alteration of physical habitat or primary production to top-down influences of predacious fishes. At the organism level, in many places there is a need for more information on the native flora and fauna as a baseline for interpretation of the impacts of non-native species. At the genetic level, hybridization appears in some cases to enhance invasiveness. For example, heterosis (hybrid vigour) may have enhanced the spread of carp and tilapia strains in Australia (Arthington, 1991; Mather and Arthington, 1991). There is a need to understand the key factors driving ecosystem resistance to invasions and their capacity to recover from invasions (Bunn and Arthington, 2002). How can the impacts of invasive species be distinguished from the consequences of other stresses such as loss of habitat and hydrological connectivity, flow regulation, loss of riparian functions and water pollution? These knowledge gaps present challenges for constructing useful conceptual models to guide the planning of experimental research, prevention, management, monitoring, and control of invasive species in inland water ecosystems.

While some may argue that 'the horse is out of the barn' with regard to tilapia because certain species are already so widespread and well established, there are rivers, streams, and estuaries in every region that have not yet experienced introductions. The prevention of further introductions as well as the control of established feral populations will go a long way towards stemming the loss of biodiversity in aquatic ecosystems worldwide.

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APPENDIX: SAMPLE OF RESEARCH ON ESTABLISHMENT AND IMPACTS OF INTRODUCED TILAPIA

Region or country	Species	Pathway	Findings/impact	Citation
Africa: Lake Victoria	<i>O. niloticus</i> (introduced) <i>O. leucostictus</i> , <i>T. zillii</i> , and <i>T. rendalli</i> remain at low levels)	Stocked	Thought to have outcompeted (habitat and trophic overlap) or genetically subsumed two native species, <i>O. variabilis</i> and <i>O. escuelentes</i> .	(Balirwa <i>et al.</i> , 2003)
Africa: Limpopo River System (border between South Africa, Botswana, Zimbabwe and Mozambique)	<i>O. niloticus</i>	Culture	Hybridization between native <i>O. mossambicus</i> and introduced <i>O. niloticus</i> and <i>O. macrochir</i> reported (loss of <i>O. mossambicus</i> genetic integrity).	(van der Waal and Bills, 2000)
Brazil (Lago Paranoá)	<i>O. niloticus</i> <i>T. rendalli</i>	Not specified	10+ years of experimentation show that tilapia enhance nutrient loading through P-excretion and P-release via bioturbation. Large-scale removal of tilapia yielded significant water quality improvement.	(Starling <i>et al.</i> , 2002)
Colombia	<i>O. niloticus</i> <i>O. spp.</i> (red hybrid tilapia)	Accidental introduction	Introduced <i>O. niloticus</i> has become one of the most important species for the fishery in the coastal lagoon Ciénaga Grande de Santa Maria. Native fish show decreasing trend.	INVEMAR data (Leal-Florez, 2003)
Nicaragua	<i>O. spp.</i>	Stocked	80% reduction of native cichlids in Lake Nicaragua. Introduction of parasites. Elimination of <i>Chara</i> spp., an important habitat for native cichlids, in Lake Apoyo.	(McKaye <i>et al.</i> , 1995; McKaye <i>et al.</i> , 1998b; McCrary <i>et al.</i> , 2001)
Madagascar	<i>O. mossambicus</i> <i>O. niloticus</i>	Aquaculture	Established and widespread. Interviews with fisherman	(Reinthal and Stiassny,

Region or country	Species	Pathway	Findings/impact	Citation
	<i>O. macrochir</i> <i>T. melanopleura</i> <i>T. rendalli</i> <i>T. zillii</i>		(Reinthal and Stiassny, 1991) indicate correlation between introduction of exotics (including tilapia) and decline of natives.	1991; Lévêque, 1997)
Philippines	<i>O. mossambicus</i> <i>O. niloticus</i>	Stocked	Nile tilapia may have contributed to the extinction of native cyprinids in Lake Lanao and the decline of the endemic sinarapan (<i>Mistichthys luzonensis</i>) in Lake Buhi. Mozambique tilapia established in all brackish water farms, rivers, swamps, and ricefields. May have contributed to extinction of endemic sinarapan.	(Bleher, 1994; Maguilas, 1999) (Pullin <i>et al.</i> , 1997)
USA: California	<i>T. zillii</i>	Biocontrol of weeds/macrophytes	Describes feral tilapia situation in CA. <i>T. zillii</i> implicated in decline of desert pupfish in Salton Sea. Has also been collected in coastal waters. Impacts on aquatic vegetation in warm months. Populations conflict with native fish restoration but are probably declining. Biology and environmental impacts of <i>O. mossambicus</i> marine populations in CA are unknown.	(Costa-Pierce, 2003)
USA: Florida	<i>T. zilli</i> <i>T. mariae</i>	Not specified	Describes hybridization between two introduced <i>Tilapia</i> spp. found in Florida.	(Taylor <i>et al.</i> , 1986)
USA: Mississippi	<i>O. niloticus</i>	Aquaculture	<i>O. niloticus</i> ranked 6th in total abundance of fish for all sites sampled (2nd in the Pascagoula/Escatawpa River systems). Adaptive feeding strategy = no direct feeding competition with native centrarchids in the study.	(Peterson <i>et al.</i> , 2002)

Region or country	Species	Pathway	Findings/impact	Citation
USA: Nevada	<i>O. aureus</i>	Not specified	Correlated with drastic decline in endangered Moapa dace and Moapa White River springfish. Predation and competition with native fish. Stomach content analyses indicated omnivory (vegetable and animal material, including native fish).	(USFWS, 2002)
USA: Pennsylvania	<i>O. aureus</i>	Aquaculture	Established population of blue tilapia in the Susquehanna River. It was the most abundant species present, was reproducing (over-wintering in thermal effluents), and was believed to pose a threat to native species. Eradication using lethal cold-shock was successful at the principal site; blue tilapia likely remain downstream.	(Skinner, 1984; Stauffer <i>et al.</i> , 1988)